ON THE RELATION OF THE FLORA OF THE LOWER SONORAN ZONE IN NORTH AMERICA TO THE FLORA OF THE ARID ZONES OF CHILI AND ARGENTINE.*

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THE relation of the flora of extra-tropical North America to that of extra-tropical South America was first discussed by Gray and Hooker in their report on "The vegetation of the Rocky mountain region and a comparison with that of other parts of the world,"[1] under the title "North American types in South America." In this report there was printed a list of some eighty genera which contained identical or more or less closely related species in the southwestern states and south of the equator, concerning which they remark:

> Clear if not very numerous indications exist that there has at some time been greater opportunity for extension of North American types into the southern hemisphere. It appears that this has taken place along the western side of the American continent, along the central part of North America and Mexico, and the western part of South America. When our cool temperate flora flourished only along or near the southern border of the United States, the warm temperate, to which most of the plants enumerated belong, was still farther south. When the climate became again warmer, a portion of these were as well placed for southward as for northward retreat.

Two years later Professor Engler[2] defined this relation of the two floras more precisely, presenting a revised list of about eighty genera, involving many species, characterized chiefly by the fact that they were elements of the Mexican plateau and

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[1] Bulletin U. S. Geol. and Geog. Surv. of the Territories **6**:—. 1880.

[2] Versuch einer Entwicklungs-geschichte der Pflanzenwelt **2**: 224. 1882.

portions of the bordering states, which, being mostly absent from south Mexico, Central America, and the Andes of Colombia, Venezuela, and Ecuador, reappear again first in Chili. Emphasis was laid upon the large percentage of Californian genera represented in Chili by identical or corresponding species, or even by species very distantly related, and their general absence in the intervening region.

These lists by no means included all the North American elements in Andean or extra-tropical South America, nor did they indicate that some very notable cases represented the extension of South American elements into extra-tropical North America, though of course these additional phenomena of distribution were discussed elsewhere in the *Entwicklungs-geschichte*, and it will be necessary to become familiar with them in the present paper.

More accurately defined the regions chiefly concerned are as follows:

1. In North America, the arid belt designated by Dr. Merriam[3] as the Lower Sonoran zone, including the Mexican tableland and adjacent western Texas, New Mexico, Arizona, Nevada, and Utah, with central, southern, and most of Lower California, approximately the region discussed by Professor Engler under "Das mexikanisches Hochland" and its northward extensions.

2. In South America, the desert of Atacama from about Cobija to 27° south and the less arid district south to 34°; the arid sand steppes and salt deserts of western Argentine along the east slope of the Andes, embracing in general from Catamarca at the north, Cordoba at the east, and Mendoza southward toward the Rio Colorado and Rio Negro; the "Chañar-Steppe" of Grisebach and "Monte Formation" of Lorentz.

With the above regions are also concerned the Gulf zone, with southern Brazil, Uruguay, and eastern Argentine; and the high Andes of Colombia, Venezuela, Ecuador, Peru, and Bolivia

[3] Geographical distribution of plants and animals, Year Book Dep. Agric. 1894: 207 (and note).

above 3000^{m}, in the latter of which a very prominent Mexican highland and boreal element occurs.

The vegetation with which we have here to deal is above all one of xerophytic stamp. It falls into the two following categories: (1) groups distributed more or less continuously along the continental axis, always interrupted by the moist tropical and subtropical belt from south Mexico to the Andes of Colombia and Venezuela (the subandine province of Engler[4]), but with a very marked development in the arid plains and plateaus of the two extra-tropical zones in question; (2) groups not at all high mountain plants, but existing both in the Chilian or Argentine arid zones and in the Lower Sonoran zone of North America, but entirely disconnected through the intervening distance. It is evident that group (2) will furnish the more interesting and difficult questions of distribution as related to genetic affinities. It is further evident that satisfactory discussion can follow only after a critical determination of what those affinities are. In the following pages the writer presents a great deal more than he has himself determined critically, recognizing also that some excellent illustrative groups are left unmentioned.

The instances cited from Amarantaceæ, Malvaceæ, Loasaceæ, and Leguminosæ are not the results of my own study, although I have been able to compare specimens in all of them. The Loasaceæ will be very fully treated in the forthcoming monograph by Drs. Urban and Gilg. Gomphrena, Malvastrum, Sphæralcea, and Prosopis deserve more special study in comparing the species of the different regions concerned. One of the very best illustrations was found in the Zygophyllaceæ, in which, of course, I have simply used the results of Professor Engler's study of the family. In the other cases I have made a rather more detailed study of the specimens in the Berlin Herbarium.

AMARANTACEÆ-GOMPHRENEÆ.

This group of the Amarantaceæ is peculiarly the New World development of the family, finding there a subtropical and warm

[4] Entwicklungs-geschichte der Pflanzenwelt 2 : 206.

temperate habitat in both North and South America. The more pronounced xerophytic genera occupy the Lower Sonoran zone in North America, and similar portions of southern Brazil, Uruguay, Argentine, and in a few cases Chili, being connected through the gulf region rather than along the Andes. Certain of the genera, as Pfaffia, Iresine, and perhaps Alternanthera, are more nearly tropical, and prevail in the territory encircling the gulf of Mexico. Three genera, Cladothrix, Gossypianthus, and Dicraurus, are confined to the Lower Sonoran zone. Guilleminea extends from this zone along the Andes to Peru, *G. densa* having the distribution of the genus. Frœlichia has several distinct species in the two extra-tropical zones, with one, *F. Floridana*, generally distributed and perhaps in both.

Gomphrena affords the most noteworthy case of distribution. Of the ninety species, more than sixty are of extra-tropical South America, more than ten are Sonoran, and fifteen natives of Australia. *G. globosa* is the cosmopolitan member. It appears that the Australian species are quite as closely related to the South American as are those of the Lower Sonoran zone, and all three regions would indicate a distribution analogous to that I have shown in the case of the Frankenia § Toichogonia-Cosmopolita.[5]

In so far as special contrivances for distribution are present they are as follows:

1. The stems are jointed and fragile, and the flowers easily disarticulate from the rachis.

2. The perianth is beset with long woolly hair in most of the genera.

3. The perianth is furnished with stout barbed hairs (*Alternanthera repens*) or with setose or spiny excresences (Frœlichia).

4. The bracts are long and spiny tipped (Gomphrena, Alternanthera).

These characters would aid the fruit in adhering to hairy or woolly mammals.

[5] Geog.-Distr. of Frank. Engler's Botan. Jahrbücher 24 : 407.

MALVACEÆ.

Three genera, Sphæralcea, Malvastrum, and Sida, furnish good illustrations for our purpose. They are pronounced xerophytic genera, and have this noteworthy feature in common, that they occur in the Lower Sonoran zone, in the South American arid regions, and either in the Capland or in Australia.[6] In Malvastrum, while the type of the three regions (Sonoran zone, Argentine-Chili, etc., Capland) appears to be a common one, there occurs in the Andes of Chili and Peru the very distinct section Phyllanthophora described by Professor Schumann[7] as follows:

In Chili, und dem Andinen Gebiete überhaupt steigen die Arten der Gattung M. hoch in die Gebirge und nehmen einen durchaus alpinen Character an; sie sind durch niedrigen, dicht rasigen Wuchs mit rosettig gedrängten Grundbl. und starke graue Bekleidung ausgezeichnet. Diese Formen haben stets Bl., welche an den Tragblättern emporgehoben sind, und aus dem Stiele derselben hervorbrechen. Sie bilden die einzige wohl abgegrenzte Gruppe, die Asa Gray als Phyllanthophora bezeichnet hat.

In this connection the distribution of several species of Sida[8] is of interest, as follows:

Sida leprosa K. Schumann (*Malva leprosa* Ortega; *Sida hederacea* Torr.).—Uruguay, Patagonia, Argentine, Cuba, Mexico, Washington to southern California, Utah, Arizona, and W. Texas.

Sida hastata St. Hil. (*S. physocalyx* Gray).—Argentine, Uruguay, Mexico, Texas to Arizona.

Sida anomala St. Hil. (*S. fasciculata* T. & G.).—Matto Grosso, Uruguay, Argentine, Bolivia, Cuba, Florida, Texas, Mexico.

[6] Sphæralcea, four species in Capland; Malvastrum, fifteen species in Capland; Sida, seventeen species indigenous to Australia (see *Pflanzenfamilien* 3^6:—). Compare in this connection Gomphrena and Frankenia.

[7] Pflanzenfamilien 3^6:41.

[8] This is being designated here the "Gulf zone distribution." Other illustrations are the following:

1. *Cienfugosia sulphurea* Garcke (*Fugosia Drummondii* Gray). Southwes, Texas, Mexico, southern Brazil, Paraguay.

2. *Spergularia Plattensis* Fenzl. Dallas, Texas, to southern California and south Brazil.

3. *Lepuropetalon spathulatum* Ell. Southern California, Georgia, Texas, Sonorat Chili, Uruguay, Montevideo.

4. *Polygala paludosa* St. Hil. Brazil, Paraguay, Louisiana, Texas.

The lack of mechanical devices for distribution in these genera seems not to have restricted them, which makes apparent the often substantiated fact that certain inherent ground gaining tendencies apparently render distribution independent of mechanical contrivances.

LOASACEÆ.

The Loasaceæ are almost exclusively a New World family, having, according to Gilg,[9] their center of distribution in Chili. The more extreme xerophytic genera spread thence over Argentine, and reaching North America find a second development chiefly in the Lower Sonoran zone. Four genera, Cevallia, Petalonyx, Eucnide, and Sympetaleia are endemic within this zone. Scyphanthus, Cajophora and Blumenbachia are southern extra-tropical. The largest genus, Loasa, furnishes many desert species for the Atacama and Argentine deserts, and while developed mostly in these regions and in the Andes, some species push north into Mexico (§ Saccatæ, 13 species, including *L. triphylla*, Peru to Mexico). But Mentzelia is the genus most conspicuous because of its distribution in the two zones under discussion, although quite abundantly distributed elsewhere, and particularly along the intervening Andes.

SEC. I. TRACHYPHYTUM, eight species; two Chili, one Chili-Argentine, one Argentine, four western North America, of which *M. albicaulis* reaches the plains and gulf coast.

SEC. II. MICROMENTZELIA, one species, *M. Torreyi*, in California and Nevada.

Sec. III. EUMENTZELIA, twenty-six species.

A. *M. aspera*, with the distribution of the genus; *M. oligosperma*, North American, east to Florida; two Argentine species.

B a. One Atacama, one California, one Florida, two Texas and north Mexico.

B b I α. Two Mexico, one Chili and Peru.

B b I β. Five Mexico, one Argentine.

B b II α. One Mexico.

B b II β. Two Mexico, one Bolivia, one Venezuela, one Colombia.

[9] Pflanzenfamilien 3^{6a}: 106. The above account of the Loasaceæ is taken from this source.

SEC. IV. DENDROMENTZELIA, one species, a large shrub or tree, Mexico.

SEC. V. BICUSPIDARIA, four Californian species, extending to Arizona and north Mexico.

SEC. VI. BARTONIA, six species.

A. Two species in western North America.

B a. One species in western North America.

B b. Three species; *M. albescens* in Argentine, Texas, and Mexico; two species in central and gulf states.

It appears from this synopsis, that although the development of the Loasacæ has proceeded in a manner to result in endemic genera in both the Sonoran zone and Chili-Argentine, still for Mentzelia, in particular, there is rather an intimate relation in distribution between the two regions.

The mechanical devices for distribution are such as to secure ready transportation by mammals or birds. The stems are exceedingly brittle, and all the younger parts are thoroughly beset with stout barbed pubescence, so that a very slight disturbance suffices to fasten the branch or capsule to the disturbing object.

LEGUMINOSÆ.

The Leguminosæ and also the Compositæ deserve special study in their distribution and relationships in the arid regions of North and South America. It suffices here simply to bring forward an illustration, and the genus selected is Prosopis, because in the remoteness of regions occupied and as a zonal genus it agrees with certain Zygophyllaceæ, *e. g.*, Larrea, Porlieria, and Bulnesia. Leaving out of account the two Asiatic and the two African species, there remain more than twenty New World species whose geographical center is in Argentine. These fall into two sections:

ALGAROBIA. Nineteen species, mostly in Argentine, but including the noteworthy *P. juliflora*, the mesquite, which in its distribution has come to occupy all of the subtropical and warm temperate, more or less arid districts of the western hemisphere. Apparently the Lower Sonoran zone would be very accurately

defined by the North American distribution of *P. juliflora*, and its occurrence in the Andes, the West Indies, etc., marks those zones which enter secondarily into the discussion of distribution between extra-tropical North and South America.[10]

STROMBOCARPA. Six species; *P. torquata*, *P. strombulifera*, and *P. reptans* in Argentine; *P. heterophylla*, *P. cinerascens*, and *P. pubescens* in the more arid portions of the Lower Sonoran zone (west Texas, Mexico, and westward). Of *P. pubescens* Dr. Merriam[11] says:

> This mesquite, commonly known as "screw bean," is widely distributed over the deserts of the southwest, usually in company with the preceding (*P. juliflora*).

While the Sonoran and Argentine species of Prosopis are more nearly related than the wide geographical separation would seem to allow, only in the case of *P. juliflora* does there seem to have been ready interchange between the regions.

The genus is favored for a wide distribution by reason of the sugary mesocarp, which makes an article of food for herbivorous animals, the hard indigestible seed being in this way carried in the alimentary canal uninjured, and left with excrement in favorable situations for germination. This is more especially the case in § Algarobia, and above all in *P. juliflora*, of which Dr. Havard[12] says:

> The ripe pod or "bean" contains more than half its weight of assimilative nutritive principles, and is therefore a valuable article of food. The most important of these is sugar, in the proportion of 25 to 30 per cent. Most herbivorous animals, but especially the horse and mule, are fond of this pod and thrive on it. In the field it is a welcome though imperfect substitute for grain. The mesquit "bean" is one of the staple foods of Mexicans and Indians.

These facts would seem sufficient to insure a very general distribution. That the Strombocarpa species are not wanting in

[10] Compare Bulnesia and Heterostachys.

[11] Shrubs of the Death Valley Exped. North Amer. Fauna 7: 300.

[12] Report on flora of S. and W. Texas. Proc. U. S. Nat. Mus. 8: 498.

[13] Op. cit. 499.

a similar quality is shown by the following, also from Dr. Havard:[13]

The twisted pod or bean contains a spongy and nutritious pulp, rich in sugar, and is used as food by the Mexicans and Indians.

POLYGONACEÆ-ERIOGONEÆ.

This group of the Polygonaceæ, embracing eleven genera, is notably characteristic of southern California and the adjacent arid regions. Kœnigia is an exception, being an arctic and subarctic species. Of the remaining ten genera, six are confined to southern and Lower California and adjacent islands. Eriogonum, by far the largest genus, is distributed over the whole of western United States, although its chief center of development is also California. Lastarriæa has one species found in both California and Chili. Oxytheca has five Californian species, of which one is in Chili. Chorizanthe embraces some twenty-five Californian species (Euchorizanthe), of which one is in Chili; while there is a peculiarly Chilian group, Chorizanthopsis, of about ten species, none of which are in California.

Southern California appears clearly the center of development of Polygonaceæ-Eriogoneæ, and the Chilian representatives, therefore, may be referred to this region for their immediate or more or less remote origin.

Lastarriæa Chilensis, although described as a Chilian plant, is evidently Californian originally. It possesses a very wide distribution in the coast and hill country of Chili, likewise throughout southern California. The plants of the two regions are so nearly identical that a very recent distribution must be supposed. This has probably occurred in connection with the shipping of stock, particularly of sheep, as the plant is especially adapted for such means of distribution (1) by the recurved hooks of the involucre, and (2) by the easy breaking off of the younger parts of the stems.

Oxytheca dendroidea Nutt. falls in the same category as *L. Chilensis* Remy; and the same may be said of *Chorizanthe com-*

missuralis Remy, which, being one of the Euchorizanthes of California, occurs in Chili without noticeable variation. All of these species are fitted especially for distribution by cattle or sheep; but by whatever means they have come to Chili, it is safe to infer (1) that they are Californian, and (2) that this distribution has occurred in very recent times.

But comparing Chorizanthopsis with Euchorizanthe, the case is fundamentally different. Any intimate connection between these sections must be referred to an age long past. This is shown by the totally different methods by which they have adapted themselves to xerophytic conditions. The Californian species are all short-lived annuals, adapted for growing in the very driest places. The whole time of growth, flowering, and maturing seed lasts but a few weeks. With the approach of rainless parching weather their work is completed.

Of the Chilian species, all are shrubby, and often in sandy places form dense patches as a means of mutual protection. They are wholly different in habit from the Californian species, and are the one exception in Polygonaceæ-Eriogoneæ where stipules are produced. This section would appear to be an offshoot from Euchorizanthe, as Oxytheca and Eriogonum are, although the change is not, as in those, within the involucre, but in the vegetative structure. In its shrubbiness Eriogonum is very similar to subgenus Chorizanthopsis. The same circumstances which witnessed the rise and spread of Eriogonum over western North America may have witnessed also a more general distribution of the group into the southern hemisphere, of which the Chilian Chorizanthes are the remnant.

It is interesting to note in connection with this group that several genera which have special devices for distribution are narrowly endemic. Pterostegia and Harfordia have the bracts developed into bladder-like structure, for wind distribution; Centrostegia has wing-like, spurred involucral bracts; Nemacaulis and Hollisteria have woolly involucral bracts and perianth; while Phyllogonum has neither bracts nor involucre. All of these are limited to southern California and adjacent

islands. Kœnigia, which has no special mechanism for distribution, is the most widely distributed of all.

FRANKENIACEÆ.[14]

The Frankeniaceæ are typically halophytic plants, represented in the new world as follows:

FRANKENIA § TOICHOGONIA-COSMOPOLITA, six species in Chili on the coast and in the alkali regions inland. Of these *F. grandifolia* is abundant on the California coast, about salt lakes of southern California, and eastward to southern Arizona, New Mexico and northern Mexico, the inland type being var. *campestris* Gray.

F. § TOICHOGONIA-ISOLATA, three species: *F. farinosa*, about Cobija in northern part of desert of Atacama; *F. triandra*, the Puna region, at 3500 to 4000^{m}; *F. vidali*, islands of San Felix and San Ambrosio, Chili.

F. § BASIGONIA, two species: *F. Palmeri*, Lower California to San Diego bay; *F. Jamesii*, east foot of Rocky mountains in Colorado and western Texas.

NIEDERLEINIA: *N. juniperoides*, salt steppes of Argentine; nearly related to *Frankenia* § *Basigonia*.

The Frankeniaceæ illustrate two features in the relation between the two regions of North and South America now under discussion.

1. That a very recent distribution has taken place in the case of *F. grandifolia*, which belongs to a section notable for the number of closely related species. This distribution may be due to birds, since the plant is found so widely distributed inland and at a considerable height above the sea (1000^{m}).

2. That *F. Palmeri*, *F. Jamesii*, *F. triandra*, and others, and *Niederleinia juniperoides* are isolated species, which we may regard as remnants of a previously widespread development; and therefore no interchange between the regions occupied has occurred under present geological conditions.

CHENOPODIACEÆ.

The Chenopodiaceæ should be considered in this connection,

[14] For detailed discussion of the geographical distribution of the Frankeniaceæ see Engler's Jahrb. **24**: 394. 1897.

notwithstanding the fact that there are many cosmopolitan species. A very useful instance is furnished by the genus Spirostachys, of which *S. occidentalis* is the North American form, occurring throughout the salt steppes of the Lower Sonoran zone; and *S. vaginata* and *S. Patagonica*, two nearly related South American species from the Argentine salt steppes, where they are abundant and conspicuous. I am inclined to believe there is no recent connection between the species of these two regions. *Heterostachys Ritteriana* merits mention here, because, aside from Spirostachys, the other nearly related genera are in the central Asiatic salt steppes and Australia; and the plant further illustrates the phenomenon of Gulf zone and southern Brazil distribution, being described from Central America, northern South America, the West Indies, southern Brazil, and Argentine.[15]

ZYGOPHYLLACEÆ.

The critical work done by Professor Engler on this family[16] makes it of special value for our purpose. He has shown that there is a very considerable development of the Zygophyllaceæ in the New World, of which the larger portion form the consistent group Guajacineæ, which is the present expression of a branching off from Old World Zygophyllaceæ in geological times. With few exceptions the Zygophyllaceæ in the western hemisphere are limited to the Lower Sonoran zone in North America and its corresponding zone in Argentine and Chili. The regions in addition are savannas of Venezuela and Colombia, southern Florida, West Indies, and southern Brazil; exactly the previously mentioned Gulf zone distribution.[17] Following is a tabular arrangement of the Zygophyllaceæ, based upon Professor Engler's study of the family:

[15] See under Malvaceæ.

[16] Pflanzenfamilien 3^4:74; Geog. Verbr. der Zygoph. im Verh. zu Syst. Glied. Abh. Kön. Preuss. Acad. Wiss. zu Berlin, 1896.

[17] Compare Prosopis, Heterostachys, and references under Malvaceæ.

	Sonoran zone, North America	W. Indies, S. Brazil, northern S. America	Chili-Argentine xerophytic zone	Means of distribution
1. Fagonia *cretica*	var. *Californica;* San Diego, Los Angeles bay, N. Mex. (val de las Palmas)		var. *Chilensis;* N. Chili (Coquimbo, Tarapaca, Atacama, etc.). var. *aspera;* Quebrada de Gaihuano.	Mucilaginous seed coat with spirally coiled projectile hairs, fitted for adhering when moistened.
2. Guajacum	*G. parvifolium;* Mexico. *G. Coulteri;* Mexico.	*G. officinale;* Fla,, Antilles, Guiana, Venez., Colombia (arid coasts). *G. sanctum;* Fla., Bahamas, Antilles, Guatemala.		Thin fleshy exocarp which birds would eat.
3. Porlieria	*P. angustifolia;* Texas, Mexico.		*P. hygrometrica;* N. Chili, Peru. *P. Lorenzii;* Argentine steppes.	
4. Pintoa			*P. Chilensis;* N. Chili.	No special mechanical device for distribution.
5. Bulnesia		*B. arborea;* a high tree in savannas of Col. and Venez.	*B. bonariensis;* Santiago del Estero; west slope of Sierra de Cordoba. *B. Schickendantzii;* Catamarca. *B. Chilensis;* Atacama. *B. foliosa;* Catamarca. *B. macrocarpa;* dune sand, campos of Catamarca. *B. Sarmientii;* Gran Chaco, Argent.	Broad winged fruit, adapted for distribution in open, arid steppes.

	Sonoran zone, North America	W. Indies, S. Brazil, northern S. America	Chili-Argentine xerophytic zone	Means of distribution
6. Plectrocarpa			*P. tetracantha;* salt regions from Catamarca to Mendoza.	Carpels with curved spines.
7. Larrea	*L. Mexicana.*		*L. divaricata;* covers exclusively great areas of Cordoba and Mendoza. *L. cuneifolia;* salt deserts, Cordoba to Rio Colorado. *L. nitida;* Argentine.	Carpels with long, thick-walled hairs.
8. Metharme			*M. lanata;* Tarapaca, N. E. Chili.	
9. Tribulus *terrestris*	In both hemispheres in warm temperate xerophytic zones.			Carpels tuberculate, or rough spiny in some cases, which would aid in transportation by mammals. Compare Malvas of a similarly wide distribution, which have no mechanical device for transportation.
	T. Californicus; S. Ariz., Lower Calif.			
	T. brachystylis; N. Mex.; Guaymas, Mexico.			
10. Kallistrœmia			*K. tribuloides;* Brazil and Argentine.	
	K. maxima; Texas, N. Mex.	*K. maxima;* Bolivian Andes northward through Central America and West Indies		
	K. grandiflora, Texas to Calif.			

	Sonoran zone, North America	W. Indies, S. Brazil, northern S. America	Chili-Argentine xerophytic zone	Means of distribution
11. Viscainoa	*V. gemmulata;* Lower Calif.			Fruit of four splitting capsules, not winged, still light enough to be carried by winds.
12. Chitonia	*C. Mexicana;* Montezuma river.			Fruits large and winged, splitting at maturity.
13. Sericodes	*S. Greggii;* N. Mexico.			Woolly carpels.
14. Peganum	*P. Mexicanum;* N. Mexico; nearly related to Chinese species.			Like Fagonia.

The distribution of *Fagonia cretica* vars., Tribulus, and Kallistrœmia is similar to that of *Frankenia grandifolia*, *Chorizanthe commissuralis*, *Oxytheca dendroidea*, *Lastarriæa Chilensis*, etc.; that of Larrea and Porlieria is like the isolated Frankenias, Spirostachys, etc. Larrea may be cited as the best case illustrating that phase of distribution in which there is absolute separation of the species both in a geographical and a genetic way. No other species are more reliable determinants of zonal areas that those of Larrea;[18] which is also to say that distribution from one zone to another over thousands of miles in which Larrea could not grow is very improbable, and this is clearly indicated by the distinctness of the species. Professor Engler expresses the opinion[19] that the present condition of Larrea, and indeed of the Guajacineæ,

[18] MERRIAM, North American Fauna 7: 293; Engler, Pflanzenfamilien 3⁴: 86.

[19] Geogr. Verbr. der Zygophyllaceæ, etc. Abh. Preuss. Akad. Wiss. —: 17. 1896.

represents remaining parts of a prehistoric, more general development, *e. g.*:

Nun haben wir bei Larrea die eigenthümliche Verbreitungserscheinung, das *L. Mexicana* Moric. vom Colorado-Gebiet Californiens, bis zum westlichen Texas und im trockneren Mexiko verbreitet ist, während drei andere Arten in den Sandsteppen und Salzwüsten Argentenien von den Anden bis Cordoba in ausgedehnten Beständen auftreten. Diese Arten sind sowohl von einander, wie auch von der mexikanischen sehr verschieden, so dass die Entstehung dieser Arten sehr alten Datums sein und eine grössere Anzahl von ausgestorbenen Arten angenommen werden muss, welche sowohl morphologische wie räumlich de jetzt lebenden Larrea-Arten mehr verknüpften.

REVIEW OF HALOPHYTIC ELEMENTS.

Following is a tabulation of halophytic species occurring beyond the tropics in North and South America. Certain endemic species of Suæda and Atriplex are believed not to be related through the cosmopolitan coast species. In no other genus, except Prosopis, are species known to occur in the intervening distance, *i. e.*, over 40° of latitude:

Lower Sonoran halophytic	Chili-Argentine halophytic
Spirostachys occidentalis.	Spirostachys { vaginata; Argentine. Patagonica; "
Suæda; *e. g.* S. Torreyana and S. suffruticosa	Suæda; *e. g.* S. divaricata.
Atriplex; *e. g.* A. canescens.	Atriplex; *e. g.* A. Chilense (Chili) (*cf.* A. cinereum; Austral.)
Frankenia grandifolia, - - = F. Jamesii, F. Palmeri, related to	F. § Toichogonia-cosmopolita; Chili.
	Neiderleinia juniperoides; Argentine.
Fagonia cretica Californica.	Fagonia cretica { Chilensis; Chili. aspera; Chili.
Larrea Mexicana.	Larrea divaricata; Argentine. " nitida; " " cuneifolia "
	Metharme lanata; Chili.
Prosopis § Algarobia; P. juliflora.	Prosopis § Algarobia; P. juliflora and many others, mostly Argentine.
§ Strombocarpa, 3 species.	§ Strombocarpa, 3 species; Argentine.

In the above will be noted (1) the greater number of common genera in Argentine and the Lower Sonoran zone; (2) that most species have no special mechanical devices for seed transportation.

BORRAGINOIDEÆ-ERITRICHIEÆ.

The Borraginoideæ-Eritrichieæ of the *Pflanzenfamilien* include seventeen genera, of which two, Lappula and Eritrichium, possess a broad distribution in the temperate zone of both hemispheres. Seven genera are chiefly E. Asiatic. Eight other genera occur in western North America, of which four recur in Chili. The geographical center of this group would appear to have been eastern Asia. From here the migration would have been along the chain of islands, Aleutian, etc., joining Asia and America, or by Behring strait and along the continental axis to extra-tropical South America; and hence the group would fall in with the boreal element represented in the Andes of Bolivia, Peru, and Chili. But the group has attained a distinct development in the Lower Sonoran zone of North America, and in the Atacama-Chilian arid zone, and for that reason is discussed here in some detail. It is to be noted that at one time or another, almost all of the west American development of Borraginoideæ-Eritrichieæ (both north and south) has been referred to the genus Eritrichium (excepting, of course, Amsinckia), and this fact may be made important in interpreting the present condition of the group in the western hemisphere. The Eritrichium type still prevails in a few species, and these are notable for being high mountain forms distributed along the continental axis from Alaska to southern Chili, with a considerable interruption from southern Mexico to Ecuador, while the forms referred to distinct genera represent apparently the variations resulting from the occupancy of a vast arid tract.

In the *Synoptical Flora* (191–199, ed. 1), Asa Gray included all of North American Borraginoideæ-Eritrichieæ under Eritrichium, Echidiocarya, and Amsinckia. In *Proc. Amer. Acad.* **20**: 264, and *Syn. Fl.* Suppl. 423–433 (ed. 2), the two latter are retained,

while Eritrichium in North America practically disappears in Krynitzkia and Plagiobothrys. Later, Professor Greene[20] defines the following genera: Allocarya, Eremocarya, Piptocalyx, Sonnea, Plagiobothrys (incl. Echidiocarya), Oreocarya, Cryptanthe, and Amsinckia. This is the arrangement adopted in the *Pflanzenfamilien*. Professor A. Philippi[21] describes one hundred Chilian species in twelve groups under Eritrichium, besides recognizing Amsinckia and Plagiobothrys. The one hundred species of Eritrichium fall under Allocarya, Eremocarya (?), and Cryptanthe.

In the following tabulation species are grouped under those characters which best emphasize the relation of the Chilian to the North American species:

	Western N. America	Chili
1. Cotyledons two-lobed AMSINCKIA. (boreal species.)	A. echinata A. intermedia } =	A. angustifolia.
2. Nutlets rugose, depressed from above; scar in middle of concave ventral face; lower leaves opposite. ALLOCARYA.	A. stricta A. trachycarpa } =	(E.) uliginosum.
	A. chorisiana A. plebeia } =	(E.) procumbens. (E.) humilis. (E.) sessifolium.
3. Nutlets very strong, thick, depressed (as in 1), very broad; stipe in middle of ventral face. PLAGIOBOTHRYS.	P. rufescens = ((E.) fulvum.)	P. rufescens. ((E.) tinctorium?)
4. Nutlets united in pairs to an elongated stipe-like base. ECHIDIOCARYA.	E. Arizonica.	None.

[20] Pittonia, pts. 1, 2, 3. 1887.

[21] Plantæ Nuevas-Chilensis, 1893.

	Western N. America	Chili
5. Nutlets with rugosity prolonged into barbed spines.	Two species.	None.
6. Nutlets with very thin, often crustaceous or pearly dotted or tubercled pericarp attached to gynobase along the whole grooved ventral face, or at base by triangular area; fitting together by plane faces. CRYPTANTHE. EREMOCARYA.	Many species.	Many species.
(1). Nutlets unlike or only one or two maturing: calyx articulated with and easily falling from rachis.	Cryptanthe angustifolia. C. crassipetala.	(E.) aspera. (E.) Bridgesii. (E.) congesta. (E.) carrizalensis. (E.) minutiflora. (E.) glareosa.
(2). Four nutlets maturing: not of extreme xerophytic habit.	Many North American species of Cryptanthe.	(E.) chætocalyx. (E.) debilis? (E.) axillare?
More xerophytic.	Eremocarya micrantha.	(Eritrichium) parviflora.
(3). Nutlets very large, protruding beyond calyx; pericarp crustaceous, silvery white.	Cryptanthe Jamesii.	(E.) gnaphalioides, and most amphicarpous species.
(4). Calyx circumscissile.	In several groups.	None.
(5). Calyx lobes with long, foliose tips, mostly thickly beset with long, needle-like hairs: more extremely xerophytic.	C. Torreyana. C. leiocarpum. C. intermedium. C. ambigua. C. barbigera.	(E.) longiseta. (E.) micrantha. (E.) calycina. (E.) diffusum. (E.) diplotrichium.
(6). Species with amphicarpous nutlets.	None.	Fourteen species.

The foregoing synopsis of characters does not always bring together plants of similar habit, as, for example, *Cryptanthe Jamesii* (N. America) and *C.* (*Eritrich.*) *gnaphalioides* (Chili), but it does aid in showing (1) that the Chilian species are an expansion of the North American development, and (2) that while identical species exist in the two zones there was also possible a distribution long enough ago to permit noticeable individuality to arise in the Chilian group.

To summarize briefly: More than 130 species of Borraginoideæ-Eritrichieæ have been described in western North America, of which over 60 per cent. are confined to the Sonoran zone. Fewer than ten of these species pass into northern Mexico; but one into southern Mexico. In the Chilian xerophytic zone, from 23° S. to 34° S., more than one hundred Borraginoideæ-Eritrichieæ have been described, of which five or six are high mountain forms of a wider distribution southward and northward, especially in the high Andes of Peru, Bolivia, and Ecuador. But there remains a region of more than twenty degrees latitude from which Borraginoideæ-Eritrichieæ are absent, or in which they occur very sparingly.

The southward extension of this group may be ascribed in part to glacial agency, inasmuch as some species belong to the high Andean boreal element. Mechanical arrangements for distribution are found in the easy disarticulation of the fruit, and its needle-like hairiness in Cryptanthe and Eremocarya; in the roughened or spined carpels of certain species; and in the long, sharp-haired calyx lobes of others.

With the Borraginoideæ-Eritrichieæ may be presented also the genus Pectocarya. The genus embraces the two sections Ktenospermum and Gruvelia.

KTENOSPERMUM has the same species, *P. linearis*, in California, Utah, Arizona, and in Chili. From California north to British Columbia is var. *penicillata*, and in Peru a similar var. *lateriflora*.

GRUVELIA has *P. setosa*, a distinctly marked species confined to southern California and Nevada. There is a more common and widely distributed form of this section which Gray added to

the Chilian *P.* (GRUVELIA) *pusilla.* It is not identical with *P. pusilla*, and to call it a variety of that species hides the essential fact that the Chilian plant is a southward migration of the common form of GRUVELIA.

The flat light carpels of Pectocarya are admirably adapted for clinging to birds or mammals because of the pectinate margin with its recurved setæ.

POLEMONIACEÆ.

The Polemoniaceæ duplicate the characteristics of the Borraginoideæ-Eritrichieæ in being a boreal group with a marked development in the Lower Sonoran zone of North America, repeated in a less marked degree in the Chilian zone. Except for the genus Gilia the family would scarcely come within the scope of this discussion, being in their South American distribution high mountain species.

Gilia includes some eighty North American species, falling under thirteen sections; and about fifteen Chilian species, mostly included in Eugilia, Navarretia, and Dactylophyllum, but, as in Cryptanthe, having an individuality of species that indicates a prehistoric as well as modern distribution.

Western N. America	Chili
§ EUGILIA.	*Gilia laciniata*, described originally from S. Amer.; occurs likewise in western N. Amer.
Gilia multicaulis, western California, is of *G. laciniata* type; straggling laciniate-leaved forms doubtless=	*G. laciniata.*
Gilia capitata and *Gilia achillæfolia* are more extreme California and Oregon species, related to - -	*G. laciniata.*
Gilia inconspicua, Wyoming to western borders of Texas, and west to California and British Columbia; forms with laciniate radical leaves very close to - - - - -	*G. crassifolia.* *G. copiapina.* *G. longifolia.*

Western N. Amerfca		Chili
		Gilia fœtida, distinct Chilian species. *Gilia glabrata* and *G. ramosissima* are Chilian species of common Eugilia type.
§ NAVARRETIA.		
Gilia intertexta, plains of Columbia river to California and the Rocky mountains - - - - -	=	*G. involucrata* (incl. *G. Navarretia* Steud., and *G. eryngioides* Lehm.).
Gilia minima, of arid portions of interior of Oregon and Nevada to Colorado and Dakota - -	=	dwarf forms of *G. involucrata* in Chili.
§ DACTYLOPHYLLUM.		
Gilia pusilla, Guadaloupe island, and var. *Californica*, Sacramento to Nevada, - - - - -	=	*G. pusilla*, in Chili.
COLLOMIA.		
Collomia linearis Nutt., Saskatchawan, Oregon, Washington, and Utah, - - - - -	=	*Collomia coccinea* Lehm., Peru, Bolivia and Chili.
Collomia grandiflora Dougl., similar to preceding, plains from Rocky mountains to California and Nevada.		
Collomia gracilis, Alaska to Chili.		
POLEMONIUM.		
Polemonium micranthum - -	=	*P. antarcticum.*

In the preceding tabulation the more extreme xerophytic species do not appear, because it is only the mountain species which have the extended distribution, and among which, therefore, the same or closely related species occur in both Chili and western North America. The method of distribution is of interest here. Commonly in the Polemoniaceæ the seed is furnished with a layer of cells whose walls become mucilaginous by contact with water, expelling forcibly the spirally thickened hair-like processes which cause the seed to adhere firmly to moistened

objects (*e. g.*, feet of birds) and thus secure transportation. So far as I was able to examine, all the South American species of Polemoniaceæ possess these mucilaginous seeds. *Gilia minima* and dwarf forms of *G. involucrata* (Chili) grow in little dense mats in arid spots. On the addition of moisture the seeds are gradually pushed up from the dense enclosure of bracts until they stand exposed and ready to adhere to any disturbing object. In the section Navarretia the bract development itself would be sufficient to bring about extended distribution by clinging to the hair of mammals. The absence of these genera from both north and south Mexico is noteworthy.

Summary.

1. Most of the genera just considered are of pronounced xerophytic or halophytic character.

2. Characteristic American groups, such as Zygophyllaceæ, Guajacineæ, Borrag.-Eritrichieæ, Amarant.-Gomphreneæ, and Loasaceæ, tend to a development in both extra-tropical xerophytic zones, often with the same, and generally with nearly related species in both zones.

3. For some genera each zone has its characteristic group of endemic species, indicating an independence from the other reaching into prehistoric time, *e. g.*, Malvastrum, Chorizanthe, Larrea, etc.

4. The halophytic genera in particular indicate that in some cases no distribution has occurred from one region to the other under present geological conditions, *e. g.*, *Frankenia Palmeri*, *F. Jamesii*, *F. triandra*, *Niederleinia juniperoides*, Spirostachys, Larrea, etc.

It is evident from a study of the plants concerned that distribution by natural methods has occurred and is occurring under present physical conditions. It is further evident that distribution has been greatly facilitated by what may be called, in contradistinction, artificial means, namely, as a result of commerce.

Again, one must suppose the present conditions, or others as favorable, to have endured far back into the history of the pres-

ent plant world to allow time enough for the isolation of such groups as Chorizanthopsis, Malvastrum § Phyllanthophora, or even for the Chilian development of Borrag.-Eritrichieæ.

But how does it occur that the high andean flora is chiefly boreal? And how have the arctic-alpine plants reached the southern high Andes from the Rocky mountains? Further, how have the sharply defined and isolated species of Larrea, Frankenia, Prosopis, etc., come to be in both regions?

Gray and Hooker supposed that in the glacial time there was a driving of boreal and warm temperate elements southward, as a result of which some plants were placed favorably for migration farther south. Engler suggests that the southward migration of animals caused by the glacial encroachment was very notable in aiding the distribution of plants southward over the isthmus.

It has been suggested that geological conditions have allowed a more general extension along the west American coast of an arid plateau similar to that of middle and northern Chili. Referring to a chart of ocean depths along the Pacific coast it is clear that by an uplift of 3000 feet a series of abrupt step-offs or shelves would be exposed extending to the Californian coast, and making the isthmus region a broad belt of land. This, besides offering a highway for xerophytic elements, would also bring about that union of the Pacific islands off the Californian coast with the continent which Sereno Watson[22] supposed must have prevailed in order to give the similarity of island flora to that of California. He suggested that the relations to the adjacent continent indicate a former flora which spread over a wide region now submerged, from which ancient flora the elements common to California and Chili were derived.

Such a condition of emergence along the west coast would be very favorable as an explanation for many of the phenomena of distribution, but I am not convinced that it is either necessary or possible to assume this. One must bear in mind that an elevation of the coast of South America by 3000 feet would in all

[22] On the flora of Guadaloupe islands. Proc. Amer. Acad. 11: 112. 1876.

likelihood mean an elevation of the Andes much higher above their present summits than we are warranted in ascribing to them. Professor Engler[23] says that the Andes of Venezuela, Colombia, and Ecuador could not have been completely glaciated during the glacial period, for in this zone we find peculiar tropical genera which, without doubt, date from the oldest times. In this event these mountains could not, within the era of present vegetation (dating presumably from somewhere in the Tertiary period) have had a much greater elevation than at present. On the other hand, there is conclusive evidence of a state of submergence during the Tertiary period and of subsequent upheaval, a fact significant in the present discussion. He says[24] in effect: If the geological conclusions be correct, we have in the Tertiary period the Andes representing an island separated from the Guiana-Brazilian triangle of land by an arm of the sea, narrow at the north, wider at the south, and from Central America by a strait. Central America was united with western North America, which latter was separated from eastern North America by inland seas. In these conditions an exchange of tropical elements between Central America, West Indies, Guiana-Brazil, and the Andes could occur. With the progress of upheaval of the Andes and consequent changes of climatic conditions the tropical nature of these mountains was modified, only those forms remaining which could adapt themselves to the extremes of greater altitude. With this elevation, in particular, the flora of the north pushed southward over a newly opened territory, peopling the Andes in such numbers that the present high andean vegetation is to be reckoned with the boreal. This southward wandering of North American species was at first of the hygrophilous elements, embracing many forms coming from the Himalayas to North America, and so explains the presence of Himalayan types in the Andes. But, as the Andes began to attain their present elevation, the moisture of the trade winds was withdrawn, and a pathway for more xerophytic elements was

[23] Entwicklungsgeschichte der Pflanzenwelt 1: 198.

[24] ENGLER: Entwicklungsgeschichte 1: 196–198.

opened, and so the xerophytic hosts, which had previously found favorable territory for expansion and variation in western North America, pressed southward; for example the Sonoran Compositæ, Polemoniaceæ, Cactaceæ, Borragineæ, etc. These, by the agency of birds and mammals, were carried over the equator to the extra-tropical regions of Chili, where again they found a broad, open territory favorable to a varied development.

Three important propositions result from the foregoing:

1. We are carried back to a time when the isolated groups, like § Chorizanthopsis and Malvastrum § Phyllanthophora could have branched off from the North American stem.

2. Conditions following the appearance of land along the eastern base of the Andes might account for a more general distribution of those genera like Frankenia, Niederleinia, Larrea, and other Zygophyllaceæ, Spirostachys, and some other Chenopodiaceæ, which are now widely separated and genetically distinct.

3. Animals, particularly birds and mammals, have probably played a prominent part in the distribution of plants across the equatorial and isthmus regions.

In the following tabulation the devices for securing distribution are brought together for a general view:

I. Adaptation for wind distribution:
   1. By winged fruits: Bulnesia, Chitonia, Centrostegia, Pterostegia, Harfordia.
   2. By light, woolly hairs: Larrea.

II. Adaptation for distribution by animals.
   1. Probably by birds.
      (*a*) As food; fleshy exocarp: Guajacum, Porlieria.
      (*b*) Seeds with mucilaginous covering and elastic coiled slime hairs: Gilia, Collomia, Fagonia, Peganum.
      (*c*) Seeds very small; without special devices for clinging, yet possibly adhering to birds' feet in mud or slime: Frankenia, Spirostachys.
   2. Probably by mammals.
      (*a*) As food; nutritious mesocarp: Prosopis.
      (*b*) By devices for clinging to wool or hair.

(1) Involucral bracts with recurved hooks; stems fragile at joints: Chorizanthe, Oxytheca, Lastarriæa.
(2) The whole plant beset with barbed hairs; stems very brittle: Loasaceæ.
(3) Rough or spiny projections on calyx or carpels: Tribulus, Kallistrœmia, some Cryptanthes, Frœlichia.
(4) Calyx with sharp, sometimes recurved stiff hairs; fruits easily falling away; many Borrag.- Eritrichieæ.
(5) Carpels flat, with hooked setæ: Pectocarya.
(6) Fruits adhering by woolly covering: Gossypianthus, Frœlichia, Gomphrena.

For most species, then, the distribution and relationships in the two zones are such as can be accounted for from data that are reasonably well established. The element which remains rests upon very much the same basis of speculation as the relation of New World to Old World Zygophyllaceæ, or Australian and South American Chenopodiaceæ, or, indeed, the relation of the great salt desert regions of the world to each other.

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